April 1944 E-615

United States Department of Agriculture
Agricultural Research Administration
Bureau of Entomology and Plant Quarantine

# NOTES ON THE BIOLOGY OF THE JAPANESE BEETLE

By I. M. Hawley, Division of Fruit Insect Investigations

## CONTENTS

## INTRODUCTION

The Japanese beetle (Popillia japonica Newman) was first found in this country near Riverton, N. J., in 1916, and by 1920 it had crossed the Delaware River and entered Pennsylvania near Philadelphia. In this earliest infested area, where the pest has now been established for at least 25 years, its behavior and its reaction to its environment have been closely studied, and the various activities of the insect are well understood. As the beetle has moved to the north or south from this center of infestation its habits and reactions have been found to change, and greater differences in behavior will probably be found as the infested area becomes larger. In part 1 of this circular certain previously unpublished data[1] dealing with the biology of the beetle in the Philadelphia area are presented; in part 2 the behavior of the insect at certain remote infested points is discussed.

[1] Data obtained at the Moorestown, N. J., laboratory in biological studies carried on prior to 1935, under the supervision of Henry Fox, have been freely used in this paper. Complete acknowledgment to Dr. Fox for the use of this valuable unpublished information is hereby given.

## PART 1. STUDIES DEALING WITH THE BIOLOGY OF THE JAPANESE BEETLE IN THE PHILADELPHIA AREA

### Distribution of stages in the soil population throughout the year as determined by soil surveys

In the vicinity of Philadelphia, where the Japanese beetle was first found in the United States, the seasonal cycle is well known. It is treated briefly in a paper by Hadley (4)[2] and in greater detail in one by Hadley and Hawley (5). The seasonal cycle is shown diagramatically in figure 1.

[2] Numbers in parentheses refer to Literature Cited, p. 18.

The status of the soil population of the beetle at various times in the year was determined by making numerous diggings and noting the number of individuals of each stage found. Each sample consisted of a section of turf 1 foot square. Systematic surveys of this type were begun in 1925 and were continued through the summer of 1936. During most of this period surveys were made at 8 locations or stations. Four of these were in New Jersey, one at Haddonfield, one at Merchantville, and two at Moorestown; the other four were in Pennsylvania, at Jenkintown, Philmont, Rydal, and Torresdale. The data on the findings in surveys during each year from 1926 through 1936 have been compiled, and the data for all 11 years have been combined in an effort to determine the approximate distribution of the stages in the soil population in an average year. There was a wide variation in meteorological conditions in this 11-year period, but, as

years with early seasons would offset those with late ones, the data as given in table 1 are believed to furnish a good idea of what to expect in an average year. However, since the surveys were usually made in open, sunny situations, the degree of development would tend to be ahead of that in certain other locations where, from shading, type of plant cover, or some other cause, the soil temperature would be lower.

During the winter months of December, January, and February, larvae in the soil are in a hibernating condition, and, as no changes from one stage to the next are taking place, the data for these three months were combined. During the period from May 11 through September 20, when changes in the soil population occur rapidly, the data were grouped by 5-day periods; at other times a 10-day interval was used. In months with 31 days, the last 6 or 11 days were considered as equivalent to the last 5- or 10-day period in months with 30 days. In this 11-year period, 37,415 samples were taken, and a total of 371,536 individuals were found.

It may be seen that as a rule about 93 percent of larvae overwinter as third instars and 7 percent as second instars; larvae that hibernate in the second stadium usually transform to the third instar during May. In the Philadelphia area larvae seldom overwinter in the first stadium; only 31 hibernating first instars were found after January 1 in the 11 years in which surveys were made. The only instar in which larvae that have overwintered and those of the new brood ever overlap is the third instar. In the 11-year period only 29 larvae from the overwintering brood were found as late as August, when larvae of the new brood were starting to reach the third instar, and none were found later than August.

In table 1 the adult is listed as a soil-inhabiting form. The reason for this is that, after transforming from pupae, beetles usually remain in the soil for several days, while their bodies and wing covers become hardened. During this short period they make up a considerable part of the soil population. Occasionally an older adult which has entered to lay eggs may be found in the ground late in the summer.

From table 1 the time when changes in the soil population should occur in an average year in the Philadelphia area can be determined. By making a few diggings at any time, it is possible to judge whether the trend is ahead of or behind that in an average year. In the 11-year period there have been years in which there has been considerable deviation from the seasonal cycle as given in table 1. For example, although normally about 93 percent of larvae pass the winter in the third instar, in 1931-32 there were 99 percent in this stage, while in the winter of 1935-36 only 78 percent had developed to this point. In 5 of the 11 years the peak 5-day period for eggs in the soil was that of July 16-20, but this high point occurred as early as July 11-15 and as late as July 26-31. The peak for pupae occurred in the June 21-25 period in 4 of the 11 years, with variations from as early as June 11-15 to as late as June 26-30. Such deviations from the normal are to be expected with most insects, and they may be explained to a large extent by variations in climatic conditions. In the Philadelphia area this fluctuation in weather may hasten or delay the starting of events in the seasonal cycle by a week or more.

Table 1.--Average percentages of individuals of the various stages of the Japanese beetle in the soil in the Philadelphia area in different periods, based on the total number of individuals found from 1926 through 1936

| Period | | Number of samples | Percent of soil population as-- | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Egg | First instar | Second instar | Third instar | Prepupa | Pupa | Adult |
| Dec.,Jan.,Feb. | | 2,045 | | 1/ * | 6.9 | 93.1 | | | |
| March | 1 - 10 | 495 | | * | 6.1 | 93.9 | | | |
| | 11 - 20 | 609 | | * | 6.5 | 93.5 | | | |
| | 21 - 31 | 1,119 | | * | 7.5 | 92.5 | | | |
| April | 1 - 10 | 1,079 | | * | 6.3 | 93.7 | | | |
| | 11 - 20 | 1,116 | | * | 6.1 | 93.9 | | | |
| | 21 - 30 | 1,497 | | * | 6.8 | 93.2 | | | |
| May | 1 - 10 | 1,454 | | * | 5.8 | 94.2 | | | |
| | 11 - 15 | 640 | | * | 6.7 | 93.3 | | | |
| | 16 - 20 | 929 | | * | 5.2 | 94.8 | * | | |
| | 21 - 25 | 883 | | * | 5.0 | 95.0 | * | | |
| | 26 - 31 | 826 | | | 2.3 | 95.3 | 2.4 | * | |
| June | 1 - 5 | 945 | | | 1.1 | 82.9 | 15.9 | 0.2 | |
| | 6 - 10 | 851 | | | 0.5 | 58.8 | 34.1 | 6.7 | |
| | 11 - 15 | 784 | | | 0.1 | 37.0 | 40.2 | 22.4 | 0.3 |
| | 16 - 20 | 893 | | | 0.1 | 24.9 | 30.9 | 41.3 | 2.8 |
| | 21 - 25 | 768 | | | 0.1 | 18.3 | 19.6 | 52.5 | 9.6 |
| | 26 - 30 | 856 | 4.4 | | | 15.2 | 11.0 | 46.6 | 22.8 |
| July | 1 - 5 | 552 | 16.9 | 0.9 | | 9.5 | 5.8 | 29.2 | 37.7 |
| | 6 - 10 | 736 | 49.6 | 1.0 | | 5.3 | 3.8 | 13.5 | 26.8 |
| | 11 - 15 | 649 | 70.3 | 3.2 | | 3.3 | 1.9 | 6.5 | 14.9 |
| | 16 - 20 | 738 | 79.9 | 10.4 | 0.1 | 2.0 | 0.8 | 2.2 | 4.5 |
| | 21 - 25 | 720 | 67.9 | 25.5 | 0.7 | 0.6 | 0.2 | 1.1 | 4.0 |
| | 26 - 31 | 818 | 43.6 | 49.6 | 4.5 | 0.6 | 0.1 | 0.2 | 1.4 |
| Aug. | 1 - 5 | 621 | 23.3 | 55.3 | 20.2 | 0.3 | * | 0.1 | 0.7 |
| | 6 - 10 | 696 | 13.9 | 47.3 | 38.2 | 0.1 | | * | 0.4 |
| | 11 - 15 | 640 | 5.4 | 32.7 | 61.1 | 0.6 | | * | 0.2 |
| | 16 - 20 | 581 | 1.4 | 23.2 | 73.5 | 1.9 | | * | * |
| | 21 - 25 | 642 | 1.6 | 17.5 | 72.2 | 8.6 | | | * |
| | 26 - 31 | 812 | 0.6 | 9.5 | 67.5 | 22.4 | | | * |
| Sept. | 1 - 5 | 517 | 0.2 | 5.2 | 49.3 | 45.3 | | | |
| | 6 - 10 | 479 | 0.3 | 2.6 | 35.6 | 61.5 | | | |
| | 11 - 15 | 701 | * | 1.8 | 29.5 | 68.7 | | | |
| | 16 - 20 | 471 | * | 1.2 | 20.5 | 78.3 | | | |
| | 21 - 30 | 1,416 | | 0.4 | 11.4 | 88.2 | | | |
| Oct. | 1 - 10 | 1,524 | | 0.1 | 7.8 | 92.1 | | | |
| | 11 - 20 | 1,439 | | 0.1 | 6.2 | 93.7 | | | |
| | 21 - 31 | 1,536 | | * | 6.1 | 93.8 | | | |
| Nov. | 1 - 10 | 1,219 | | * | 5.5 | 94.5 | | | |
| | 11 - 20 | 1,050 | | * | 6.9 | 93.1 | | | |
| | 21 - 30 | 1,069 | | * | 8.4 | 91.6 | | | |

1/ An asterisk (*) indicates that a few individuals in the given stage were found in this period. The number was always less than 0.1 percent of the total population and is not considered in computing percentages.

In the 11-year period the earliest dates of finding individuals in the various stages were as follows: Egg, June 26, 1930; first instar, July 2, 1930; second instar, July 19, 1934; third instar, August 6, 1934; prepupa, May 20, 1936; pupa, May 29, 1933; and adult, June 12, 1933.

Changes in the depth of the soil-inhabiting stages during the year

In the 11-year period from 1925 through 1935, records were obtained on the depths at which 213,037 individuals in the various stages were located. Observations were made during every month of the year, but records were often interrupted during the winter because of the frozen ground. All surveys were made in permanent turf at the same 8 stations that were used to determine the status of the soil population. In making diggings the soil was removed in successive 2-inch layers, and a record was kept of the number of individuals in all stages present in each layer. The combined findings in these examinations during the 11 years are given by 10-day periods in table 2. In months with 31 days the last 11 days are considered as equivalent to the last 10 days in 30-day months.

The records for the 3 winter months, when no change of position normally takes place, are grouped together. An idea of changes in the depth of the various soil-inhabiting stages during the normal year may be obtained by comparing the distribution as shown in table 1 with depth records in table 2.

During hibernation larvae are most plentiful at a depth of 2 to 4 inches; over 90 percent are between 2 and 6 inches at this time. The soil becomes warmer late in March or early in April, and when a temperature of about 50°F. is reached, larvae leave hibernation, move higher, and start to feed. A month or longer is usually required to complete this upward movement. Prior to changing to prepupae early in June, larvae again move somewhat deeper, cease feeding, and make the change to pupae within an earthen cell. Soon after beetles issue from the ground, they mate and start laying eggs. Most of these eggs are in the top 3 inches of the soil; in two years, for which data are available, 86.0 percent and 87.6 percent were in the upper 2 inches. As the eggs hatch, the resulting larvae start feeding on the roots of the grass close to the surface of the ground, and they continue to feed here until fall, when the downward movement to a hibernating position gets under way. At the start of this change of position the mean soil temperature is usually around 60°F.; when the temperature about the larvae reaches approximately 50°F. they become inactive. In the Philadelphia area this quiescent period usually continues uninterrupted from fall until spring; in only one year for which records are available did the soil temperature become high enough for larvae to leave their hibernating position during the winter months. It is evident that a greater proportion of larvae were deeper during the last 10-day period of August than in the preceding and following periods. The reason for this appears to be that in two of the earlier years many extra surveys were made late in August and, as rainfall was deficient in these years, larvae were somewhat deeper than in other years.

Table 2.--Average depth distribution of the soil population of the Japanese beetle in the Philadelphia area, in terms of average percentages found at five different depths, based on the number of individuals found from 1925 through 1935

| Period | Individuals involved | Percent at depth of-- 0-2 inches | 2-4 inches | 4-6 inches | 6-8 inches | 8-10 inches |
|---|---|---|---|---|---|---|
| Dec., Jan., Feb. | 15,501 | 4.7 | 61.8 | 30.7 | 2.7 | 0.1 |
| March 1 - 10 | 3,715 | 6.3 | 64.1 | 28.1 | 1.6 | 0.0 |
| 11 - 20 | 5,269 | 8.4 | 70.2 | 19.6 | 1.7 | 1/ * |
| 21 - 31 | 9,138 | 18.4 | 57.2 | 22.5 | 1.8 | * |
| April 1 - 10 | 8,737 | 34.3 | 44.3 | 19.7 | 1.6 | 0.1 |
| 11 - 20 | 7,854 | 64.9 | 28.6 | 6.2 | 0.3 | 0.0 |
| 21 - 30 | 7,994 | 88.4 | 9.6 | 1.9 | * | * |
| May 1 - 10 | 5,920 | 95.3 | 4.6 | * | | |
| 11 - 20 | 7,814 | 96.4 | 3.6 | * | | |
| 21 - 31 | 7,634 | 94.3 | 5.7 | * | | |
| June 1 - 10 | 8,345 | 85.6 | 14.2 | 0.2 | | |
| 11 - 20 | 6,053 | 71.7 | 28.2 | * | | |
| 21 - 30 | 5,436 | 69.9 | 30.0 | 0.1 | | |
| July 1 - 10 | 3,711 | 76.1 | 23.9 | 0.0 | | |
| 11 - 20 | 4,112 | 84.5 | 15.4 | * | | |
| 21 - 31 | 5,109 | 91.7 | 8.3 | 0.0 | | |
| Aug. 1 - 10 | 5,439 | 97.4 | 2.6 | * | | |
| 11 - 20 | 7,291 | 95.2 | 4.8 | 0.0 | | |
| 21 - 31 | 11,377 | 89.8 | 10.2 | * | | |
| Sept. 1 - 10 | 8,635 | 93.7 | 6.3 | 0.0 | | |
| 11 - 20 | 9,048 | 92.8 | 7.2 | 0.0 | | |
| 21 - 30 | 10,789 | 93.9 | 6.1 | * | | |
| Oct. 1 - 10 | 10,382 | 85.0 | 12.5 | 2.3 | 0.2 | * |
| 11 - 20 | 8,398 | 65.6 | 27.2 | 6.8 | 0.4 | 0.0 |
| 21 - 31 | 9,493 | 37.3 | 49.6 | 12.4 | 0.6 | * |
| Nov. 1 - 10 | 7,331 | 13.5 | 61.5 | 23.5 | 1.4 | 0.2 |
| 11 - 20 | 6,047 | 8.7 | 66.5 | 23.0 | 1.7 | 0.0 |
| 21 - 30 | 6,465 | 7.5 | 65.9 | 25.4 | 1.2 | * |

1/ An asterisk indicates that a few individuals have been found at the given depth during this period. The number was always less than 0.1 percent of the population.

Changes in larval position appear to be regulated by the overturn in soil temperatures. During the winter the temperature at the lower depths is higher than near the surface, but as air temperatures become higher in the spring the surface layer gains heat more rapidly and soon is warmer than the deeper strata. In the fall this action is reversed; in both spring and fall the vertical movement of larvae tends to accompany this soil-temperature change.

Larvae of the Japanese beetle do not hibernate at as great a depth as do those of many other scarabaeids. In the 11-year period covered by the records in table 2, only 56 larvae were found below an 8-inch depth, and in 5 of the 11 years larvae were never found below this depth. All surveys in this series were made beneath turf. In cultivated fields and gardens, and in overgrown, weedy land, larvae are normally deeper than in turf, probably because the soil is looser and easier to dig through, and the roots, which serve as larval food, go deeper. In general, the depths at which larvae are found do not appear to vary greatly in different parts of the country. Larvae have been found in the northern and southern ranges of the insect at about the same depth as in the Philadelphia area. Under real dry conditions larvae in sandy soil amid grass of a coarse, deep-rooted type have sometimes been found much deeper than would normally be expected. This is not always the case, however, for in other extremely dry situations larvae have been found near the surface, where they collected to feed on the roots of coarse types of grass and other plants.

## Changes in the abundance of the soil-inhabiting stages from year to year as indicated by soil surveys

Information as to changes taking place in the soil-inhabiting population of the Japanese beetle in any location can best be obtained by making soil surveys or diggings at regular intervals. If these surveys are made in sufficient numbers and are limited to a relatively small area with uniform topography, a good indication of abundance and of the transformations taking place can be obtained. Most of the larger changes in numbers are due to climatic influences, the actions of which are understood, but it is difficult to explain the smaller fluctuations.

As the Japanese beetle has dispersed into new areas, the population density has usually passed through a definite series of changes. Starting with the arrival of a few beetles, the infestation gradually builds up over a period of years to a strong peak; this high level is maintained for several years, after which a decline takes place. By 1926 beetles had already been present for some years at the New Jersey survey stations and a reduction in numbers was under way. For this reason the soil populations at the more recently infested Pennsylvania stations were higher than at points in New Jersey. Table 3 shows the average numbers of individuals of the soil-inhabiting stages of the Japanese beetle present in a square foot of turf in the spring and fall of each year from 1926 through 1936, at a typical survey station in each State. At least 100 square-foot diggings were made during most of the fall and spring survey periods, and in some years over 200 diggings were made. Apparently larvae were more numerous in certain spring-survey periods than in those of the preceding fall. This is obviously the result of faulty sampling, due in some cases to a shift in the survey site.

Table 3.--Trends in the soil population of the Japanese beetle at two stations in the Philadelphia area in the years from 1926 through 1936, as shown by comparing the average population in a square foot of turf in the period from September 1 to November 30 of any year with that of the period from March 1 to May 31 of the following year

| Place | Time of surveys | 1926 -27 | 1927 -28 | 1928 -29 | 1929 -30 | 1930 -31 | 1931 -32 | 1932 -33 | 1933 -34 | 1934 -35 | 1935 -36 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Merchantville, N. J. | Fall | 17.9 | 14.4 | 18.3 | 2.9 | 4.7 | 18.2 | 8.6 | 6.0 | 13.6 | 17.9 |
| | Spring | 14.3 | 9.3 | 17.1 | 2.0 | 6.9 | 16.4 | 7.8 | 5.9 | 8.8 | 2.8 |
| Jenkintown, Pa. | Fall | ---- | 21.3 | 34.2 | 32.3 | 21.3 | 25.9 | 14.4 | 14.2 | 20.3 | 7.0 |
| | Spring | ---- | 24.0 | 30.3 | 18.2 | 19.5 | 24.9 | 8.9 | 11.2 | 9.7 | 3.6 |

In a paper by Fox (1) it was pointed out that there was little mortality among larvae of the Japanese beetle during the unusually cold winter of 1933-34. In this same paper it was noted that there was little evidence of high winter mortalities in the survey records of years prior to 1934. These conclusions are largely substantiated by the data in table 3. In another paper Fox (2) showed that, in the years from 1927 through 1934, the soil population was reduced an average of 32.5 percent between the peak period in September and the end of the following May, but that only an insignificant part of this reduction took place during the winter. Mortality was highest after larvae became active in the spring just prior to pupation. As may be noted from table 3, there was a heavy mortality at Merchantville during the winter of 1935-36, when the soil population was reduced from 17.9 per square foot in the fall to 2.8 in the spring. This destruction of larvae was unanticipated, and when numerous dead larvae were found in early spring surveys an effort was made to determine the cause of the mortality. Apparently it was due largely to an unusual set of weather conditions, in which the type of precipitation and the degree of soil moisture were more important than the soil temperature. At the start of an extremely cold period there was snow on the ground at survey sites in Pennsylvania, but in New Jersey the precipitation was largely in the form of rain; the mortality was lower in Pennsylvania, for at Jenkintown the drop in population was only from 7.0 per square foot in the fall to 3.6 in the spring. The winter killing in 1936 is treated in a paper by Hawley and Dobbins (9). From table 3 it would appear that there was a considerable reduction in the soil population during the winter of 1934-35; the cause of this drop in numbers is not apparent from our meteorological records.

A marked rainfall deficiency during midsummer, when eggs of the Japanese beetle predominate in the soil, is invariably followed by a drop in the larval population. This was so in New Jersey in the summer of 1929, when there was only 6.85 inches of rain, about half the normal, during June, July, and August. The drop in the soil-inhabiting stages at Merchantville from 17.1 per square foot in the spring of 1929 to 2.9 in the fall of that year is attributed to this cause. This dry condition was limited largely

to New Jersey. No marked reduction in numbers was found in surveys in eastern Pennsylvania. In the summer of 1932 there was a less pronounced but widespread dry period which was largely responsible for the drop in the population from 16.4 per square foot in the spring to 8.6 in the fall at Merchantville and from 24.9 per square foot to 14.4 at Jenkintown. Thundershowers are common in this part of the country during warm summer days and, as the area covered by these is often small, there may be wide differences in the rainfall at places only a few miles apart. A shower at the critical time may have an important influence on egg survival and larval abundance. Soils vary greatly in their ability to hold moisture; sandy soils are poor in this respect, while heavy loams and clays hold moisture very well. The type of soil, therefore, influences the survival of eggs and the resulting beetle population in places where the rainfall is deficient in some years.

Larvae of the Japanese beetle are able to endure submersion in water for relatively long periods. Observations have been made from central New England to North Carolina at points where streams have overrun their banks and submerged infested areas from 2 days to several weeks. In no case was there any indication of marked larval mortality. This was true of larvae in a dormant as well as those in an active condition. Larvae that were submerged for several months in flooded cranberry bogs suffered no ill effects.

In some situations the concentration of larvae may be influenced by their horizontal movement in the soil. This is especially true in fallow ground, when larvae move about in search of food. It was found by Hawley (6) that a few larvae moved over 5 feet both in fallow ground and through grass in bins set up in a greenhouse; the average distance covered was greater in the fallow soil. In a series of tests in field plots, both with and without grass, Hawley (7) found (in June 1934) that the average movement during the larval stage in fallow ground was 51.0 inches, nearly three times that of 17.4 inches through grass. The greatest distance traveled in fallow land was 114 inches, as compared with 34 inches in turf. Under normal field conditions lateral larval movement will doubtless depend on the availability of plant roots as food, the soil texture, and the degree of soil moisture. If these conditions are all favorable, little movement will take place.

Systematic surveys were discontinued in 1936. Since then there have been other years with summer rainfall deficiencies, and the present population density of the insect at most points in this area is well below that of 1936. The mortality during the winter of 1935-36 and the subsequent dry summers have contributed to the reduction in numbers, but the most important factor is believed to be the destruction of larvae by milky diseases. In the last 7 years these bacterial pathogens have destroyed an increasingly large number of larvae each year throughout the Philadelphia area.

The selection of oviposition sites and the influence of this choice on the size of larval populations

If larvae of the Japanese beetle are present in large numbers in any situation, it is because this place was found to be favorable for egg deposition by adult beetles during the summer. In general, a good stand of closely cut or grazed turf is highly preferred for egg laying, but even where there is an abundance of good grass some eggs will be laid in other situations. It would appear that many factors influence the selection of oviposition sites, some of the most apparent of which are the proximity of favored food plants, the nature of the plant cover, and the degree of soil moisture.

In all types of habitat larvae tend to be the most numerous near favored food plants, since many beetles, after feeding, enter the nearby soil to deposit eggs. Under urban conditions larvae will normally be more plentiful in turf near rose bushes, grapevines, early apple trees, and other preferred hosts than at a distance from such plants. The feeding habits and food plants of the Japanese beetle are discussed in a paper by Hawley and Metzger (8).

In 1934 and 1935 a total of 4,505 square-foot diggings were made in a heavily infested farming area in southern New Jersey in an effort to determine the relative abundance of larvae in pastures and in fields planted in crops of various kinds. The average larval population in pastures was 15.2 per square foot. In fields with crops on which the beetle feeds the counts were as follows: Alfalfa, 7.2 per square foot; asparagus, 9.1 per square foot; and corn, 6.6 per square foot. In fields planted to crops on which the beetle does not normally feed the counts were as follows: Peppers, 4.6 per square foot; potatoes, 5.1 per square foot; and tomatoes, 3.8 per square foot. There was a wide variation in larval abundance, even in fields planted to the same crop. When larvae were unusually abundant in a field, it was often because the field was adjacent to fields with preferred hosts. There was a variation of from 2.1 to 26.0 larvae per square foot in asparagus fields; in those with the higher counts there had been an abundance of tall brush, which is favored as food, or there had been many preferred weed hosts because of lack of cultivation. In cornfields there was a variation of from 2.1 to 11.7 larvae per square foot; the fields with high larval populations were those in which there had been extensive feeding on the silk during the period of beetle flight. Larval counts were usually low in late-planted cornfields that did not produce silk until the numbers of beetles were reduced. The surveys in cornfields showed that larvae tend to be more abundant in the hills than in the furrows between them, especially in years with deficient rainfall.

Survey data show that some larvae are usually present in fields planted to crops on which the beetle does not feed. The abundance of larvae in a field of this type can often be explained by the location of the field. This, however, is not the sole governing factor, for, when beetles are flying in all directions on warm summer days, they have been observed to drop suddenly and to dig between clumps of earth in fields of all kinds, regardless of the crop grown. Larvae were particularly abundant

in cultivated fields in the fall of 1934, following a dry egg-laying period, in which the soil in pastures was so dry and hard that it was more difficult for beetles to enter the ground here than in the fallow, cultivated fields. Under drought conditions, oviposition is usually concentrated in low or shady places, where the ground is soft because it retains more moisture, and larvae will be plentiful in those locations the year following egg deposition. In urban communities, where watering of the grass in dry periods is commonly practiced, larvae may be so concentrated in low areas of this type that the turf will be severely injured.

Japanese beetles often gather in large numbers and feed on the foliage and flowers of clover and alfalfa. If the plants are mature and there is a thick growth at the time of feeding, few eggs will be deposited in the fields. If larvae are numerous in an alfalfa or clover field, it is usually because the beetles were present in considerable numbers when the field was recently cut. In general, beetles do not choose for oviposition a place with high, dense plant growth. Neglected land overgrown with tall weeds is not usually considered favorable for beetle development, and yet there are several places of this type, in both the northern and southern ranges of the insect, where the beetle is not only established but has built up strong isolated colonies. In most places of this type there is an abundance of favored weeds for food, but a good stand of turf, which was once considered essential for the beetle to thrive, is entirely lacking. It is becoming more evident each year that the Japanese beetle is a very adaptable insect that can survive and become a pest under a wide range of environmental conditions.

Seasonal trends in beetle abundance as shown by the use of traps

In the years from 1926 through 1932, traps were operated near Moorestown, N. J., to obtain information on the abundance of the Japanese beetle during the summer. The same type of trap and the same kind of attractant were used throughout this period, and most of the 21 to 24 traps were placed in the same location each year. Data on catches in 5-day periods from June 15, when traps were put out, until September 15, when they were removed, have been compiled. In table 4 is shown the proportion of the total season's catch that was taken in each 5-day period.

There is much irregularity in the records of the various years. In 1 year the peak period occurred as early as mid-July, while in 2 other years it took place in mid-August. When the data for all 7 years are combined they indicate that in an average year beetles reach their peak late in July and maintain a condition close to the maximum for about 3 weeks. The most important factor influencing the trap catch in any 5-day period is the weather during that period. If beetles do not fly they will not be taken in traps, and their flight is governed almost entirely by such factors as temperature, relative humidity, sunlight, and wind velocity. In general, the conditions most favorable for a high catch are a temperature of 85° to 95°F., a relative humidity below 50 percent, plenty of sunlight, and a moderate wind. If ideal conditions continue throughout a 5-day period in midsummer the catch could run into considerable numbers, while in 5 days of cloudy or rainy weather only a few beetles would be taken.

Table 4.--Seasonal distribution of Japanese beetle adults in the Philadelphia area, in successive 5-day periods, in terms of percentages of the total catch by the use of traps

| Periods | Relative proportion of population | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1926 | 1927 | 1928 | 1929 | 1930 | 1931 | 1932 | Average |
| June 15 - June 19 | | | | | 1/ * | * | | * |
| June 20 - June 24 | | | | * | * | * | * | * |
| June 25 - June 29 | * | * | * | 0.6 | 0.1 | 0.1 | 0.2 | 0.1 |
| June 30 - July 4 | 0.1 | 0.1 | 0.1 | 1.7 | 1.0 | 0.6 | 1.4 | 0.5 |
| July 5 - July 9 | 0.6 | 0.6 | 0.9 | 9.1 | 5.2 | 1.5 | 4.4 | 2.5 |
| July 10 - July 14 | 2.9 | 3.0 | 0.7 | 18.9 | 4.7 | 6.8 | 14.9 | 6.5 |
| July 15 - July 19 | 3.8 | 6.8 | 8.5 | 6.7 | 12.6 | 5.3 | 10.5 | 7.1 |
| July 20 - July 24 | 16.1 | 4.6 | 7.0 | 10.6 | 16.4 | 14.5 | 4.6 | 9.2 |
| July 25 - July 29 | 12.0 | 29.9 | 12.2 | 17.1 | 13.8 | 31.2 | 5.8 | 19.8 |
| July 30 - Aug. 3 | 7.5 | 12.4 | 21.4 | 14.3 | 17.1 | 17.4 | 16.2 | 14.1 |
| Aug. 4 - Aug. 8 | 16.4 | 14.4 | 15.0 | 8.4 | 18.8 | 10.6 | 12.6 | 13.8 |
| Aug. 9 - Aug. 13 | 25.6 | 18.3 | 12.7 | 6.2 | 5.0 | 4.4 | 16.8 | 15.0 |
| Aug. 14 - Aug. 18 | 9.6 | 3.5 | 11.0 | 3.2 | 1.6 | 5.4 | 7.5 | 5.8 |
| Aug. 19 - Aug. 23 | 0.1 | 2.0 | 5.1 | 1.5 | 1.2 | 0.6 | 3.0 | 1.9 |
| Aug. 24 - Aug. 28 | 3.0 | 0.5 | 3.2 | 1.1 | 1.1 | 0.8 | 1.3 | 1.4 |
| Aug. 29 - Sept. 2 | 1.8 | 1.8 | 1.8 | 0.4 | 0.8 | 0.6 | 0.5 | 1.3 |
| Sept. 3 - Sept. 7 | 0.2 | 1.8 | * | 0.1 | 0.3 | 0.1 | 0.2 | 0.7 |
| Sept. 8 - Sept. 12 | 0.2 | 0.2 | 0.3 | 0.1 | 0.2 | 0.1 | 0.1 | 0.2 |
| Sept. 13 - Sept. 15 | 0.1 | 0.1 | 0.1 | * | 0.1 | * | * | 0.1 |
| Total catch | 999,276 | 2,012,285 | 682,821 | 739,049 | 386,560 | 588,006 | 694,490 | 6,102,487 |

1/ An asterisk indicates that a few beetles were found in this period, but the total was less than 0.1 percent of the total catch of the season.

Trap-catch data were used to determine the number of days, after the first beetle was taken, that would be required to obtain various percentages of the entire season's catch. As based on the combined records of the 7 years, these were as follows: 1 percent, 14 days; 10 percent, 23 days; 20 percent, 28 days; 30 percent, 31 days; 40 percent, 36 days; 50 percent, 38 days; 60 percent, 41 days; 70 percent, 44 days; 80 percent, 47 days; 90 percent, 51 days; and 95 percent, 58 days. In the 7 years there was a variation of about 10 to 14 days between the earliest and latest dates for reaching any percentage of the total catch. As traps were removed about September 15, when a few scattered beetles were still present, no information is available as to how late beetles could have been taken. It is evident from table 4 that by mid-September the catches were greatly reduced, but occasional beetles were sometimes found during October in the Philadelphia area.

In the 7-year period 15 traps were at exactly the same position each year. The total yearly catches in these traps were as follows: 1926, 812,719; 1927, 1,169,675; 1928, 518,992; 1929, 526,687; 1930, 290,937; 1931, 433,617; and 1932, 543,650. These traps were all in or near Moorestown, N. J., which is close to the original center of infestation in this country. Apparently the peak in beetle abundance in this particular area was reached in 1927. There was a marked deficiency in summer rainfall in this area in 1929 at the time that eggs of the beetle would be present in the soil, and the decreased trap catch in 1930 is believed to have been due to the mortality of eggs during this period.

## PART 2. OBSERVATIONS ON THE BEHAVIOR OF THE JAPANESE BEETLE AT REMOTE INFESTED POINTS

### Seasonal cycle at points north of the Philadelphia area

North of the earliest infested area about Philadelphia spring comes later, summers are cooler, and the cold days and frosts of fall come earlier. Climatic differences of this type have a direct influence on the seasonal cycle. In average years at points in northern New Jersey, southeastern New York, southwestern Connecticut, and the lower Connecticut River Valley the effect of these differences is shown by the appearance of the first beetles from 1 to 2 weeks later and a tendency for them to be present longer in the summer and early fall. In this area there are more larvae in the first and second instars during hibernation. As these small larvae must complete their development before changing to beetles, the time during which the adults are emerging from the soil is prolonged. In the general region about New York City, however, the variation from the seasonal cycle about Philadelphia is not marked. Development in a late season in the early-infested area would not differ radically from that in an early season in the vicinity of New York. Emergence of adult beetles is slightly later on eastern Long Island and along Long Island Sound than farther inland. This delayed emergence has also been noted at seashore points along the coast of New Jersey, where summer temperatures average lower than at points away from the coast.

In the more northern and western portions of Massachusetts and in southern New Hampshire and Vermont, where the beetle is now present in several isolated colonies, the seasonal cycle is quite different from that of the Philadelphia area. There has been a strong local infestation at Keene, N. H., for several years, and the behavior of the insect was under close observation there in 1936 and 1937. In these years the infestation was restricted largely to three contiguous, well-kept properties, where favored food plants were plentiful and an abundance of suitable turf was available for egg deposition. Information as to the behavior of the beetle at Keene and other New England points was obtained by making soil surveys at various times during the year and by operating experimental plots in which eggs from caged beetles were placed beneath turf at intervals during the summer. These plots were placed at a point just beyond the edge of the infested area where there would be little chance of eggs being deposited in the plots by stray beetles.

In southern New Hampshire the active season for the soil-inhabiting stages of the Japanese beetle is about 5 or 6 weeks shorter than in the Philadelphia area. Beetle emergence usually starts early in July, about 3 weeks later than in the earliest infested area, and egg deposition is later in getting under way. Soil temperatures in summer are lower in New Hampshire, and as a result the growth rate of eggs and larvae is slower than farther south. Frosts occur early in the fall, and a soil temperature of 50°F., which is about the point at which larval feeding and movement ceases, is reached several weeks in advance of the time it occurs in the Philadelphia area.

From 39 diggings, each 1 foot square, made in the most heavily infested yard at Keene between September 8 and October 20, 1936, the development by stages of the 838 individuals found at the beginning of the hibernation period was as follows: Eggs, 14.1 percent; first instars, 23.4 percent; second instars, 40.3 percent; new third instars, 21.1 percent; and old third instars of the 1935 brood, 1.1 percent. Old and new third instars differ markedly in appearance and size and may be easily separated. In April and May of 1937, eggs and larvae in all three stages were found in surveys in about the same proportion as in the fall. The eggs were killed during the winter, for, although they were still plump and appeared healthy, they soon collapsed and disintegrated when taken into a warm room.

The results obtained from two experimental plots, each 4 by 4 feet, set out in turf at Keene in 1937, with eggs obtained from caged beetles, are also of interest. The larvae in a plot started August 29, with eggs laid between August 19 and 29, hibernated as first instars about one-third grown. The 85 third instars recovered when the plot was dug up on July 6, 1938, were dark in color and still feeding, indicating that they should have been able to transform to beetles by late August. Apparently few, if any, eggs hatched in a plot started September 21, 1937, with eggs deposited between August 29 and September 21, since no larvae could be found when the plot was dug up on July 7, 1938.

The main points in the seasonal cycle as found at Keene in 1936 and 1937 were as follows: Both eggs and newly hatched larvae were present at the beginning of winter. Eggs cannot stand freezing temperatures, and all these were killed; newly hatched larvae cannot endure freezing until they have fed and made some growth, and most of these also perished. Larvae of the second instar predominated in the hibernating population, some had reached the third or final stadium, but many were still of the first instar. The degree of development reached by larvae at Keene depends to a large extent on the time and place of egg deposition. Larvae from eggs laid in July by the first beetles to emerge will usually reach the third stadium by fall and will attain the adult stage by the following July. Larvae from eggs laid during the first half of August will largely hibernate as second instars and emerge as beetles early in August of the following year, at which time the adult beetle population is at or near its peak. Eggs laid late in August should be able to hatch, and the larvae should be able to make sufficient growth for survival before winter sets in. By September the soil temperatures have usually fallen so low that eggs deposited at that time are usually killed and there is little chance of their hatching. If a few late-deposited eggs do hatch, soil temperatures will usually be so low that the small, frail larvae will not feed and so will perish. The seasonal cycle for Keene, as outlined above, is based on observations in only 2 years and may not be representative of all years. It was evident that the degree of larval development was influenced by the type of location in which larvae occurred. In places that were shaded part of the day, larvae showed less development at any given time than did those in more open, sunny situations.

By the end of August in 1936 the adult beetles were greatly reduced in numbers at both Keene and Concord, N. H. Early in September a new, fresh-looking lot of beetles appeared at both points, and these continued until killed by a heavy freeze about September 27. Nothing definite is known as to the source of these late-issuing beetles, but probably they came from larvae that wintered as first instars and, because of low soil temperatures, did not become adults until September. No prepupae or pupae were found in surveys at Keene late in August or in September, but a few larvae of the previous year's brood were found at this time. These were mostly in shady situations, and, as they were never at all numerous, it is not surprising that prepupae or pupae were not found. One pupa was found in Concord late in August. Many of the eggs found in surveys in September and October 1936 were doubtless laid by late-emerging beetles. There was no evidence of a late emergence at Keene in 1937, but late peaks of this type in beetle abundance have been reported in several years by State agencies that have operated traps in New England. The reason for the difference in beetle behavior at Keene in 1936 from that of 1937 is probably to be found in the temperature records for the 2 years. In 1936 air temperatures there were close to normal from June through August, while in 1937 they were above normal; in August the mean temperature was 5.4 degrees above normal. The higher temperatures in 1937 probably hastened larval development and brought all beetles through by the end of August.

Observations on the Japanese beetle in northern Japan have shown that some individuals require 2 years to complete their life cycle. It has been felt that this would be the case in the more northern parts of this country. There was no evidence of the occurrence of a 2-year cycle in southern New Hampshire in either 1936 or 1937. If the larvae of the previous year's brood found at Keene and Concord in August and September 1936 had held over until the following year, they would have had a 2-year cycle. To have such a cycle, they would have had to pass the second winter still in the larval stage, since many prepupae and pupae are killed when exposed for a short time to a temperature no lower than 40°F. Even under the heavy coating of snow that is normal to this part of New England, the soil temperature will be close to the freezing point for several months every year. The summers of both 1936 and 1937 at Keene were close to or warmer than normal. In a short, cool summer, larvae would develop more slowly than in these 2 years, and a 2-year cycle for some individuals might be possible. At the present time there is no known place in this country colder than Keene where the Japanese beetle is present in sufficient numbers to permit a study of the reaction of the insect to extreme climatic conditions. When such a situation is found, it is conceivable that a 2-year cycle may be observed.

It is evident that even in the warm developmental seasons of 1936 and 1937 an appreciable portion of the soil-inhabiting population of the Japanese beetle was lost through the destruction of eggs and immature larvae by low temperatures in the fall. It appears certain that some such loss must occur every year at points as far north as southern New Hampshire and that the degree of population reduction in any year will depend on seasonal climatic conditions. It is conceivable that this reduction could be of enough importance to prevent the Japanese beetle from becoming as numerous and destructive as it is farther south. It is far too early to attempt to predict the future behavior of the insect in its extreme northern range, but there is some evidence that the build-up in the colony centers in northern New England has not been as rapid as that in more southern ones.

Seasonal cycle at points south of the Philadelphia area

South of the Philadelphia area the emergence of the adult beetles starts earlier, the growing season for soil-inhabiting forms continues longer, and hibernation starts later than farther north. Observations at infested points in southern Virginia show that beetle emergence normally starts there early in June, about 10 days earlier than about Philadelphia, and that nearly all individuals enter the winter as fully grown third instars. As a result of this uniformity in development the subsequent transformations of the soil-inhabiting stages tend to take place about the same time. This results in beetles issuing over a shorter period and the intensification of the feeding of the adults, but a shortening of their feeding period. In southern Virginia it would appear from soil surveys that no larvae change to prepupae prior to hibernation. It is doubtful whether prepupae and pupae could survive winter even as far south as Virginia.

There are points south of Virginia where Japanese beetles have been found in small to moderate numbers, but, either owing to the limited number present or because an effort is being made to destroy the insect at most of these colony centers, there has been little chance to study closely the changes taking place in the soil-inhabiting population. Information as to the times that adult beetles are present at these places is available, however, from records of trap catches. Each year trapping is carried on by the Division of Japanese Beetle Control of the Bureau of Entomology and Plant Quarantine, in cooperation with State agencies, at many points in the outer zone of spread.

By using data as to the time that emergence has started in previous years in the area near Philadelphia, and the temperature conditions which brought it about, an attempt is being made to develop a procedure for predicting the time when Japanese beetles will start to emerge at points in the outer zone of spread. This work is not complete, but from the data so far obtained it would appear that in the coastal regions in States south of Virginia the emergence of Japanese beetles as determined by trap catches tends to be somewhat later in starting than would be anticipated from temperature data for these places. The reason for this apparent retardation in emergence is not entirely clear.

The future status of this beetle as a pest in portions of the southern coastal area is still in doubt. Such factors as high soil temperature in summer, low rainfall, the time spent in hibernation, and the plant material available for larval food may play a part in regulating the build-up of colonies and the ability of the insect to survive. It is possible that the beetle may have to pass through a conditioning process to adapt it to the new environment before the population builds up to the destructive point. Rearing studies have shown that the insect is able to live and thrive in many common southern soil types, when adequate moisture and suitable food are available. Recent studies carried on at the Moorestown, N. J., laboratory under temperatures approximating those of Miami, Fla., indicate that there could be two broods a year at this point for some of the Japanese beetle population. That this might be the case was predicted by Fox (3).

At the higher elevations in the western portions of the Southern States the climate is similar to that farther north, and the beetle will doubtless react there as it does under corresponding conditions in the North. For example, at Asheville, N. C., with an elevation of 2,193 feet, Japanese beetles are present in considerable numbers, and the seasonal cycle has been observed to approach that found in New Jersey.

Seasonal cycle at points west of the Philadelphia area

To the west of the earliest infested area about Philadelphia the seasonal cycle of the Japanese beetle is not expected to vary radically from that at comparable points in the East, except where the climate may be influenced by mountains or large bodies of water. At infested points along the shores of the Great Lakes in New York and Middle Western States beetles issue about 2 weeks later than about Philadelphia; at points some distance south of the lakes emergence may be as early as, or earlier than, in the early-infested area.

There are few places in the Middle Western States where Japanese beetles are now present in numbers at which control measures are not being employed. From the scant information available it appears that the Japanese beetle is capable of becoming a serious pest throughout this region, except possibly at a few points where the summer rainfall is often deficient.

## LITERATURE CITED

(1) FOX, H.
1935. Some misconceptions regarding the effects of the cold of February 1934 on the larvae of the Japanese beetle, _Popillia japonica_ Newman. Jour. Econ. Ent. 28: 154-159.

(2) ------
1937. Seasonal trends in the relative abundance of Japanese beetle populations in the soil during the annual life cycle. Jour. N. Y. Ent. Soc. 45: 115-126, illus.

(3) ------
1939. The probable future distribution of the Japanese beetle in North America. Jour. N. Y. Ent. Soc. 47:(105)-123.

(4) HADLEY, C. H.
1940. The Japanese beetle and its control. U. S. Dept. Agr. Farmers' Bul. 1856, 22 pp., illus.

(5) ------ and HAWLEY, I. M.
1934. General information about the Japanese beetle in the United States. U. S. Dept. Agr. Cir. 332, 23 pp., illus.

(6) HAWLEY, I. M.
1934. A preliminary report on the horizontal movement of grubs of the Japanese beetle. Jour. Econ. Ent. 27: 503-505.

(7) ------
1935. Horizontal movement of larvae of the Japanese beetle in field plots. (Horticultural Inspection Note) Jour. Econ. Ent. 28: 656.

(8) ------ and METZGER, F. W.
1940. Feeding habits of the adult Japanese beetle. U. S. Dept. Agr. Cir. 547, 31 pp., illus.

(9) ------ and DOBBINS, T. N.
1941. Mortality among hibernating larvae of the Japanese beetle with special reference to conditions in the winter of 1935-36. Jour. N. Y. Ent. Soc. 49: 47-56, illus.

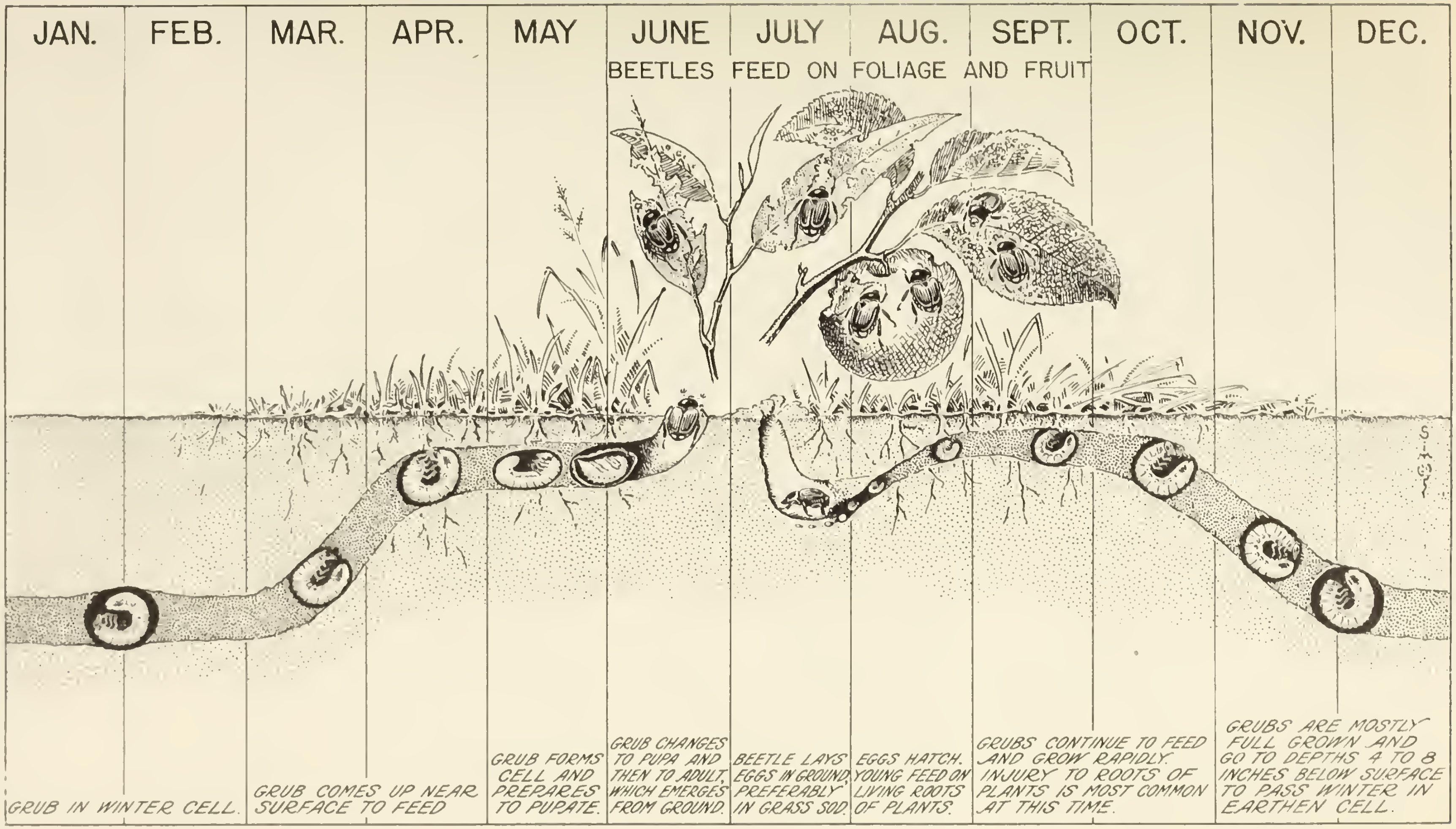


Figure 1.--Diagrammatic representation of the seasonal life cycle of the Japanese beetle in the Philadelphia area.